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The effects of aperiodic desiccation on the diversity of benthic desmid assemblages in a lowland peat bog

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Abstract The lowland minerotrophic "Swamp" peat bog, located in the Czech Republic, is one of the most important European sites of desmidiacean diversity. The hydrological regime of the bog is driven by the water level of a nearby ancient manmade pond. Therefore, the bog experiences severe aperiodic drying events related to the pond draining. In this study, we investigated the drought-related response of the benthic desmid assemblages of the bog. The samples were taken bimonthly from 12th May 2008 to 19th May 2010, including the 8-month drying out period between October 2008 and June 2009. In addition to the species frequency data, morphometric methods were used to analyse the disparity, morphological turnover and surface-to-volume (S:V) ratios of Desmidiales. The drying event influenced the species composition, biovolume and S:V ratio data of the more species-rich pool, but its influence was less conspicuous in the species-poor acidic site. Accordingly, the species-rich site had generally higher species or morphological turnover between successive samples. The indicators based on the morphometric data were generally more sensitive than the species data. Therefore, we propose that the biovolume, S:V ratios or disparity measures of desmidiacean assemblages might be of benefit for future studies of peat bog microphytobenthos. Desmid assemblages at both sites recovered rapidly following the re-wetting of the bog, and they attained the pre-disturbance diversity, species composition and disparity values. We conclude that the drying event of the bog did not irreversibly influence its valuable desmid assemblages.

Keywords Desmidiales · Species diversity · Geometric morphometrics · Microphytobenthos · Peat bogs

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Introduction

Drying events and the related desiccation stress are considered one of the important factors controlling the distribution and diversity of phytobenthos in freshwater wetlands. For example, Gottlieb et al. (2005, 2006) illustrated that localities differing by the length of the annual dry period in the subtropical Everglades wetland system (Florida, USA) had significantly different species compositions. In addition, the long dry period sites better coped with non-periodic events of severe drought (Gottlieb et al. 2005). Benthic diatoms were found to be influenced by the periodic seasonal drying events of the wetland sites (Gell et al. 2002; Lane et al. 2009), but their community structure and conservation value (evaluated by the different indices of biotic integrity) reflected more strongly other environmental factors, such as eutrophication, indicating the well-established adaptive mechanisms of these benthic microalgae to seasonal hydrological regimes (Lane et al. 2009). By contrast, there was a strong response of benthic diatom communities to the long-term changes in hydrological regime signified by more pronounced dry periods (Gaiser et al. 1998).

Green algae belonging to Desmidiales (Streptophyta) dominate the phytobenthos, especially acidic peatland habitats (Brook 1981). They also strongly reflect the desiccation gradient. Coesel (1982) illustrated how long-term terrestrialisation leads to a decrease of biradiate, compressed forms with highly structured cells, such as species of the genera *Micrasterias* or *Euastrum* in Dutch lowland freshwater wetlands. By contrast, drier, semi-terrestrial conditions were correlated with a high proportion of cylindrical forms, such as species of the genus *Actinotaenium* or other unicellular Zygnematophyceae (the genera *Mesotaenium* and *Cylindrocystis*). A similar pattern of the long-term response of desmid communities to peat bog drainage was also reported by Wayda (2004). Borics et al. (2003) found desmids more sensitive to drying events than diatoms in Hungarian acidic bogs and bog lakes so that the impoverishment of the phytobenthos species composition usually starts with the disappearance of most Desmidiales. Similarly, Gottlieb et al. (2006) illustrated that the diversity of the so-called "soft algae", i.e. green algae and non-silicified stramenopiles, was more related to the length of the hydroperiod and driven by water depth. Mataloni (1999) investigated the ecology of microalgae in temperate bogs of Tierra del Fuego, Argentina. She also reported that desmids generally reduced their frequencies along the long-term desiccation gradient and that their species richness reduction was contrasted by the increase in dominance of the species present in the drier extreme of the gradient. However, no studies have so far been published on the effects of non-periodic, unexpected severe drought on phytobenthos of peat bogs.

Desmidiales have repeatedly been used as a model group in peatland ecology (Brook 1981; Coesel 1982; Krasznai et al. 2008). Most notably, Coesel (2001, 2003) developed an elaborate system for the evaluation of wetlands based on the species composition of desmid communities. His nature conservation value (NCV) index includes three separate series differing in their acidities with each one constituting a gradient from a disturbed to stable wetland habitat. Each desmid species is assigned by a value of rarity (r) ranging from 0 (commonly occurring) to 3 (very rare). In addition, Coesel (2001) also rated each species by a sensitivity value (s) ranging from 0 (not indicative, wide ecological amplitude, particularly encountered in pioneer communities or under disturbed environmental conditions) to 3 (most indicative; the species in question is proper to highly structured with finely balanced ecosystems). The sums of the s and r values of all the desmid species occurring in a sample, together with its species richness, constitute a basis for acquiring the final I value of the index (for details see Coesel 2001, 2003). The s and r values of the

desmid NCV index were originally designed for the Netherlands, but Fehér (2007) and Šťastný (2010) adjusted the values of individual species for central European lowland wetlands. Since its introduction in 2001, Coesel's desmid NCV index has gradually been established as one of the most efficient methods for the ecological assessment of peatlands (Fehér 2007; Ngearnpat and Peerapornpisal 2007; Krasznai et al. 2008; Šťastný 2009).

The present study is based on species composition data and the species frequencies of Desmidiales acquired during a 2-year investigation at the "Swamp" Natural Reserve, Czech Republic. The study was concentrated on the temporal variation of benthic desmid communities following the anthropogenic, extreme drought event at the locality. This minerotrophic peat bog locality has repeatedly been the subject of phycological research since the beginning of the twentieth century. Pascher (1910, 1939) described a number of chryso- and xanthophycean algal species new to science from this locality. Mattauch (1936) published a comprehensive biodiversity account of microalgae at the locality. In addition, several new dinophycean and green algal species, and some rare pennate diatoms were also discovered and taxonomically described here (Nováková and Popovský 1972; Pfiester and Popovský 1979; Stojanovski and Kalina 1989). Recently, Šťastný (2009) investigated the desmid assemblages of this locality and reported a very rich desmidiacean flora comprising 203 species, including some extremely rare species such as *Micrasterias oscitans*, *Pleurotaenium simplicissimum* and *Euastrum pinnatum*. Consequently, the locality has been proposed as one of the most important desmid localities in Central and Eastern Europe (Šťastný 2009, 2010). Since 1972, the bog with an area of 1.45 ha has been protected by law as the only natural reserve in the Czech Republic protected primarily for the conservation of its microalgal biodiversity. In 2009, the area of the reserve was significantly expanded so that it now comprises several peatlands and fen pools in the vicinity of the core site. The investigated peat bog is entirely minerotrophic (i.e. nourished by groundwater), and the hydrological regime is driven by the water level of the nearby manmade Máchovo pond (=Der Hirschberger Grossteich). Actually, the lake shore is located only about 30–50 m from the central parts of the wetland. Therefore, the peat bog experiences irregular drying events caused by the release of water from the Máchovo pond during the fish harvest of that locality. These drying events have been rather irregular during the second half of the twentieth century. In the last decades, it dried out in 1996, then again in 2003/2004 and, for the last time, from the end of September 2008 to the end of May 2009. This study concentrates on this most recent drying event at the locality to evaluate the possible disturbance effect of this anthropogenic, 8-month drought period on the benthic desmidiacean assemblages. Two sites largely differing by their phytobenthos species composition were chosen for long-term monitoring—an acidic pool with a pH level <5.5 and a more basic site with pH > 6.5. The study was aimed to obtain more general conclusions about the response to irregular drying events of the desmidiacean assemblages in peatlands. This might be especially relevant for lowland peatland habitats in European anthropogenic landscapes, where water levels more or less depend on human agricultural or conservational activities.

Two parallel approaches were used for the identification of desmidiacean diversity patterns. Firstly, traditional taxonomic diversity data were analysed using frequencies of individual species. Secondly, morphological disparity data were used for the evaluation of the morphological diversity of investigated assemblages. The morphological disparity of a natural assemblage is acquired from the total shape variability of its species (Roy and Foote 1997). In this study, we used the 3D morphometric registration of desmid cells as a basis for 3D elliptical Fourier analysis according to Neustupa et al. (2009). These morphometric data were also used for the estimation of cell sizes and the surface-to-volume

(S:V) ratios of individual species, and, consequently, of the mean values of these indicators in individual samples.

To summarize, we asked the following questions:

(a) Was there any long-term, or even irreversible, change in species composition and the diversity indicators of desmid assemblages at the locality following the non-periodic, 8-month drought period?
(b) Did the desmid-based NCV index of the investigated sites fluctuate in relation to the drought period, and was there a complete recovery in the months following the re-wetting of the bog?
(c) Which species indicated the possible change in desmid species composition following the drying event at the locality? Were there any explicit trends in cell sizes and S:V ratios following the drought period and subsequent re-wetting?

Materials and methods

Localities and sampling

The "Swamp" bog (altitude 265 m a.s.l., total area 11 ha) is a remnant of an ancient glacial lake embayment. Since 1366, when the manmade pond was established at the site of the original wetland, the hydrological regime of the peat bog has been driven by the pond water level. The present day wetland is a lowland minerotrophic transitional bog. The hydrochemical conditions are related to the distance from the lake, varying from acidic and oligotrophic habitats (pH < 4.0) to rather mesotrophic pools with pH > 6.5. The detailed description of the environmental conditions at the locality can be found in Št'astný (2009). Two major pools of the peat bog were selected for temporal monitoring. Pool 1 (50°34′33.43″N, 14°40′15.81″E) is located in the acidic part of the reserve, whereas Pool 2 (50°34′41.77″N, 14°39′41.19″E) forms a main water body in the mesotrophic part. At each locality, we sampled 0.25 m^2 quadrates of a phytobenthic community. The samples were collected by squeezing till dry and subsequent rinsing of ca. 25 g of mosses, plants and decomposing organic matter at the site (Coesel 1982). Both localities were sampled bimonthly from 12th May 2008 to 19th May 2010, yielding two sets of 13 consecutive samples. The samples from under the snow cover were taken after careful removal of the snow layer, which was subsequently piled up back on the surface of the pools. The climatic data were acquired from publicly available sources for the Prague-Ruzyně station (see at http://www.tutiempo.net/en/), and the values of individual climatic parameters entering the analyses were deducted as a mean value of 30 days preceding the sampling date. The pH and conductivity values were measured in the field directly at the sampling localities using a combined pH/conductometer (WTW 340i, WTW GmbH, Weilheim, Germany). The probes were submerged so that they these values were always measured 2–3 cm over the bottom of pools. The pH and conductivity values were not measured in the three sampling dates when both localities were completely dried out. The 25 ml of samples were immediately fixed using Lugol's solution (3–4% final concentration). In total, 200 cells in each sample were photographed in the course of systematic inspection of the slides at the 400× magnification. The occasional long filaments of several trichal desmid species were counted up to 10 cells. The Olympus BX51 light microscope and Z5060 digital micro-photography equipment were used.

Species data analysis

Each set of samples consisted of 2,600 objects representing desmid species (200 for each sampling date). They were determined using standard taxonomic and identification monographs (Růžička 1977, 1981; Lenzenweger 1996, 1997, 1999; Coesel and Meesters 2007). The patterns of species composition among samples within each locality were illustrated using non-metric multidimensional scaling (NMDS) with a Bray–Curtis relative abundance based species distance measure in PAST, ver. 2.01 (Hammer et al. 2001). The coefficients of determination (r^2) were computed for each axis to determine what proportion of variance of the scaled data was accounted for by the NMDS procedure. Robustness of the ordination patterns was evaluated by repeated NMDS analyses using limited data sets with rare species (i.e. frequency less than 1%) omitted. These ordination patterns were compared using the *protest* function of the *vegan* package in *R*, ver. 2.6.1. (Oksanen et al. 2008). This method uses the Procrustes superimposition to rotate a matrix (i.e. ordination scores of a data set) to maximum similarity with a target matrix (i.e. ordination scores of a data set with rare species omitted) by minimizing sum of squared differences. The Procrustes rotation is typically used in comparison of ordination results and has been recommended for comparing different ordinations in multidimensional scaling (Peres-Neto and Jackson 2001). Significance of the Procrustes statistics was evaluated by a permutation test (with 1,000 permutations) on the correlation statistics derived from the symmetric Procrustes sum of squares in *protest* function (Oksanen et al. 2008). The Kruskal–Wallis tests were used for comparing relative abundances of species in drought and wet periods. Given the small number of samples, the *P*-value up to 0.10 was accepted to test for differences between the median values. The temporal autocorrelation of species composition and the correlation of species data with abiotic factors were tested by two-matrix Mantel tests (Fortin and Gurevitch 1993). The species data were represented by their frequencies used for computing the Bray–Curtis distance matrices of samples. Alternatively, the Jaccard presence–absence similarity matrices were also used. The abiotic factors were represented by the Euclidean distance matrices. Temporal variation in desmid assemblages was illustrated by the turnover index of species composition between the pairs of samples for frequency data (Tokeshi 1990; Rauch et al. 2006):

$$s_\tau = \frac{\sum_{i=1}^{n} |p_i(t) - p_i(t+1)|}{2}$$

where $p_i(t)$ and $p_i(t + 1)$ represent the frequency of a species i at time t and $t + 1$, respectively, and n is the total number of species occurring in either sample. Values of s_τ range from 0 to 1 denoting a variation in species composition from no change (identical samples) to a complete change (no species occurring jointly in both samples). The values s and r of the desmid NCV index for each sample were calculated following Coesel (2001), and using the values of individual species adjusted for the Czech Republic by Šťastný (2010). The SIMPER method (Clarke and Warwick 2001) in PAST, ver. 2.07 with the Bray–Curtis distance measure was used to identify species that characteristically discriminated between drought and wet periods (i.e. whose frequency trends reflected the drought event) at each locality.

Morphometric analyses

For each species, cell shape was registered with 144 2D landmarks placed regularly along the outline of mature cells in frontal view in TpsDig, ver. 2.15 (Rohlf 2010). Their shape in lateral view was then approximated using the algorithm introduced in Neustupa et al.

(2009). The procedure involves data on the width-to-thickness ratios of individual species for the approximation of the lateral views in biradiate desmids, and the calculation of the position of the third lobe using the position of landmarks along the outline in a frontal view in triradiate species. For examples of 3D outlines reconstructed by this method see Neustupa et al. (2009). The size-standardised coordinates of the 286 landmarks placed in the frontal and lateral views of the cells were subjected to 3D elliptical Fourier analysis in EFA3D, ver. 1.0 (Rohlf 2003) with the apical tip of a semicell as the starting point for the computation of Fourier coefficients. In total, coefficients of the 25 harmonic functions spanned the shapes of investigated species and were used in further disparity analyses.

A principal component analysis based on the variance–covariance matrix of the coefficients of the 25 harmonic functions was used to simplify the multivariate set of each locality. For further analyses, 10 PC axes spanning 99.8% (Pool 1) and 98.0% (Pool 2) of the variation were used. The multivariate sets of 2,600 objects for each locality characterised by their scores on the PC axes constituted the morphospaces for the disparity analyses. These were conducted by computing the partial morphological disparity (PD) values of individual samples. The PD, a frequently used measure of morphological diversity (Foote 1993; Zelditch et al. 2004), indicates the contribution of a sample to the overall morphospace (represented by the set of 13 temporally successive samples of each locality in this case). The PD values were calculated using the well-known Foote index (Foote 1993; see also Neustupa and Němcová 2007; Neustupa et al. 2009). The sum of the PD values of all 200 objects from each sample provides the PD of a sample (i.e. the contribution of a particular sample to the total morphological disparity of an entire set). In parallel, the sample disparity was calculated as the sum of the Euclidean distances in the morphospace between all the 200 objects belonging to a particular sample. This measure gives the extent of sample morphological disparity with no direct regard to the other samples of the locality. The morphological turnover, intended as a comparative measure to the species turnover index, was calculated for each pair of successive samples at each locality as the Euclidean distance between the sample means in the morphospace.

The size of the cells was expressed as their biovolume that was directly acquired from the landmark data. In triradiate species (e.g. in most *Staurastrum* spp.), the volume of 3D landmark configurations was assessed by $1.5k - 5$ tetrahedrons spanned by the k landmarks placed along the frontal and lateral cell outlines. Similarly, surface values were acquired by computing the areas of $2k - 4$ triangles given by the k 3D landmarks. Subsequently, the estimation of the S:V ratios of individual species was based on these surface and volume values acquired from morphometric data. Surfaces and volumes of biradiate species with generally ellipsoidal or cylindrical layouts were approximated using algorithms taking into account the extensive lobulation of desmid cells (see Supplementary material). The relationship among species diversity, morphological disparity measures and climatic factors was evaluated by linear correlation analyses with the permutation P-value based on 10,000 randomisations. The relationship between the turnover indices of both localities was evaluated by permutation t-tests (10,000 randomisations).

Results

Abiotic and species data

There were clear differences in pH and conductivity values between both investigated localities (Supplementary Table 1). Pool 1 had a consistently lower pH (mean pH 5.3

(±0.39)) than Pool 2 (mean pH 6.8 (±0.24)). Significance of this difference was illustrated by the *t*-test ($t = -10.2$, $P < 0.0001$). However, in Pool 1 there was a temporary increase in pH values related to the drought period, when pH reached 6.1 in September 2008, shortly before the complete drying event. There were similar trends in conductivity, and Pool 1 had consistently lower values (*t*-test, $t = -2.56$, $P = 0.019$), with the exception of measurements conducted shortly before and towards the end of the drought period. Climatically, there was a difference between the relatively mild winter of 2008/2009 (concurrent with the drought period) and the 2009/2010 winter, when January and February temperatures dropped significantly below long-term means. Consequently, there was a snow covering the investigated localities for 30 days prior to the January 2010 sampling date. The total number of days with snow cover was more than 50% higher in 2009/2010 than in the preceding year (Supplementary Table 1).

Desmid assemblages were clearly different between both localities in all pairs of samples. Only five taxa out of the total of 108 occurred at both localities during the two-year investigation (Supplementary Tables 2, 3). The dominant species of the desmid community in Pool 1 were acidophilic species such as *Tetmemorus granulatus*, *T. laevis*, *Micrasterias jenneri* and *Closterium striolatum*. Several rare species that were considered indicators of stable acidophilic localities by Coesel (2003) were also present, such as *Micrasterias oscitans*, *Cosmarium ralfsii* and *Xanthidium armatum*. The most frequent species of Pool 2 were *Closterium calosporum* var. *brasiliense*, *Closterium dianae*, *Cosmarium difficile*, *Cosmarium pseudoretusum* and *Staurastrum pseudotetracerum*. The rare species *Micrasterias pinnatifida*, *Haplotaenium rectum*, *Euastrum ansatum* var. *rhomboidale* and *Cosmarium pseudoretusum*, indicating a stable and valuable mesotrophic fen habitat, were also present. Interestingly, the desmid assemblages of Pool 1 (acidic site) were not temporally autocorrelated (Mantel test, B–C index, $R = 0.16$, $P > 0.05$; Jaccard index, $R = 0.22$, $P > 0.05$), i.e. the successive samples were not more similar in respect to their species composition than those sampled over a longer time period. By contrast, there was a distinct positive temporal autocorrelation of desmid assemblages in the mesotrophic Pool 2 (B–C index, $R = 0.33$, $P = 0.007$; Jaccard index, $R = 0.23$, $P = 0.024$). The NMDS ordination plots of both localities suggested the effect of desiccation on the species compositions of desmids (Fig. 1). These patterns were not significantly affected by omission of rare species as the correlations of Procrustes rotations between original and reduced configurations were high (Pool 1: $r = 0.93$, $P = 0.001$; Pool 2: $r = 0.99$, $P = 0.001$). There was also an apparent difference between the drought-related responses of individual pools. The drought period samplings from the acidic Pool 1 were clearly less different from other samples of this locality than in case of the more pH-neutral Pool 2. In Pool 1, the second ordination axis distinguished the drought period samples (Fig. 1a), together with the samples taken on September 2008 (shortly preceding the drying event) and January 2010 (the mid-winter sample taken from under the snow and ice cover). Pool 2 had the drought period samples distinguished along the first ordination axis, and these were well discerned from the others (Fig. 1b).

There was a consistently higher diversity of desmids in the mesotrophic Pool 2 than in the acidic oligotrophic Pool 1 (Fig. 2a). The temporal trends of species richness data were closely similar to those of other diversity indices, such as the Shannon–Wiener or Simpson indices (data not shown). The diversity of desmid assemblages at both localities was obviously influenced by the drought period. There was a drought-related increase in the number of species in Pool 1 ($r = 0.74$, $P = 0.006$), whereas the species richness in Pool 2 reached its minimum at the end of the drought period in May 2009 ($r = -0.71$, $P = 0.009$). The Kruskal–Wallis tests identified species, whose frequencies were

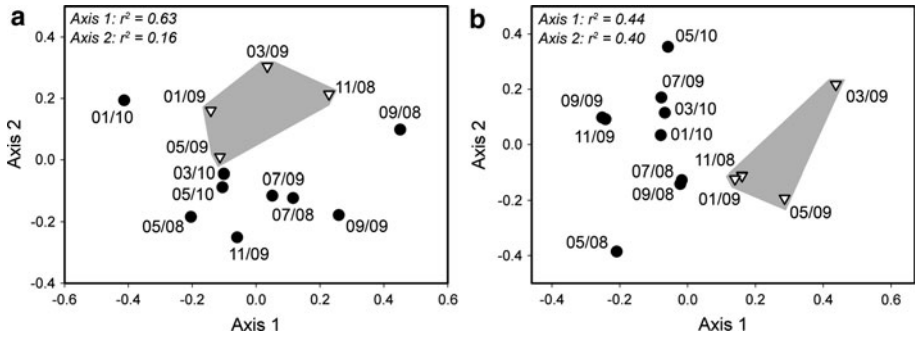

Fig. 1 The NMDS ordination plot of samples based on their species composition. **a** Pool 1, acidic site; **b** Pool 2, pH-neutral site. The *circles* correspond to the wet period samples, the *triangles* illustrate the drought period samples. The *grey section* encircles the drought period samples. The r^2 values determine proportion of variance accounted for by the ordination procedure

significantly related to the drought/wet gradient (Supplementary Tables 2, 3) and, in parallel, the SIMPER method was used to illustrate species that were primarily responsible for differences between desmid communities of dry and wet periods in both pools (Supplementary Table 4). Frequencies of *Closterium juncidum* and *Staurastrum simonyi* were positively related to the drought period in the acidic Pool 1. Conversely, *Tetmemorus granulatus* significantly decreased in relation to the drying event of the locality. Interestingly, there were several species in Pool 1, whose frequencies were possibly related both to the 2008/2009 drying event, as well as to the prolonged freezing of the pool. We can see that *Tetmemorus laevis* declined in relation to the desiccation, but its frequency was also lower in the mid-winter sample of January 2010 (Fig. 2b). A similar trend was also observed in *Closterium striolatum*. By contrast, *Xanthidium armatum*, *Micrasterias jenneri* and, to a lesser extent, *M. oscitans* displayed different patterns with relative maxima in the winter periods, and with prolonged high relative proportions in the drought period of the winter and spring season 2008/2009 (Fig. 2b). As illustrated by the Kruskal–Wallis tests, there were several species whose frequencies significantly increased following the drought period in mesotrophic Pool 2. Among them, *Cosmarium botrytis* var. *tumidum*, *C. paragranatoides*, and *Pleurotaenium trabecula* were the most conspicuous (Fig. 2c). Other species with similar patterns were e.g. *Cosmarium granatum* and *Euastrum pectinatum*. There was often also a slight second frequency peak of these species in the winter period in 2009/2010. Some species, such as *Actinotaenium turgidum*, peaked in a single sample during the drying event, but their frequencies remained low in other dry period samples so that their relation to the dry/wet gradient was not significant (Fig. 2c). By contrast, *Closterium calosporum* var. *brasiliense*, *Desmidium swartzii*, and *Staurastrum tetracerum* declined significantly in relation to the desiccation of the mesotrophic Pool 2 (Fig. 2d). At the same time, there were several rarer species with similar patterns (e.g. *Micrasterias pinnatifida*, *Staurastrum crassangulatum* or *Teilingia granulata*), but their dynamics was not supported by the Kruskal–Wallis tests. Temporal autocorrelation, i.e. the time-related, non-periodic change in species composition of mesotrophic Pool 2, may be illustrated by the continuous decrease of *Staurastrum pseudotetracerum* and *Staurodesmus dejectus* var. *apiculatus* and, by contrast, the increase of *Cosmarium humile* and *C. contractum* (Fig. 2e). In addition, *Closterium dianae* also continuously decreased at the locality, and *Staurastrum manfeldtii*, *S. alternans* and *Cosmarium angulosum* showed similar time-related increasing

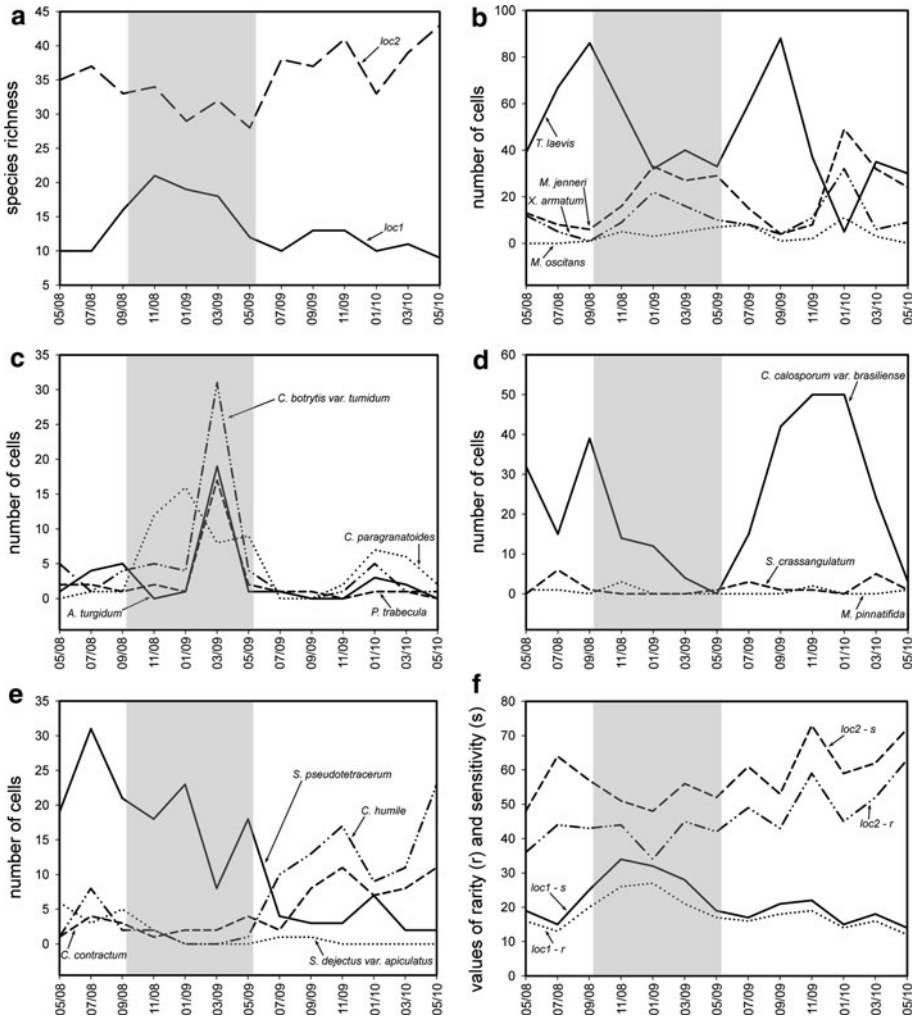

Fig. 2 The temporal dynamics of different species compositions based on the characteristics of samples. **a** Species richness, **b** frequencies of selected species from Pool 1, **c–e** frequencies of selected species from Pool 2, **f** rarity and sensitivity values of the NCV index. The *grey section* emphasizes the drought period

patterns as *C. humile* and *C. contractum*. We should also note the frequency pattern of *Hyalotheca dissiliens* that sharply proliferated after the re-wetting of the locality, and then subsequently decreased to the pre-desiccation quantities.

The sensitivity and rarity values of the NCV index varied among the samples, partly in relation to the desiccation period (Fig. 2f). There was an increase in Pool 1 (acidic site), apparently related to higher species richness resulting in higher sums of sensitivity and rarity values. On the other hand, there was a slight decrease in Pool 2, followed by a continuous increase after re-wetting. In both localities, desiccation period changes were relatively rapidly followed by the reconstitution of original values. There was generally a higher species turnover between successive samples of the assemblages in the mesotrophic Pool 2 than in the acidic Pool 1 (t-test, $t = 3.79$, $P = 0.001$, permutation P-value $= 0.0009$). In the later pool,

drying event did not lead to higher species turnover, which, by contrast, increased in the November to January samples of the 2009/2010 winter (Fig. 3a). On the other hand, desiccation and the subsequent re-wetting apparently increased the sample-to-sample species change in Pool 2, followed by a relatively more stable period with lower turnover rates. There was a moderately significant relation of temperature data with species composition in the acidic Pool 1 (Table 1) and this correlation was stronger if climatic data were expressed as the number of frost days or the number of days with snow cover. However, there were only three species whose relative proportions in the desmid community significantly correlated with temperature data. Whereas *Tetmemorus laevis* frequencies were positively related to mean temperature ($r = 0.69$, $P = 0.009$), two species had a negative temperature relationship: *Micrasterias jenneri* ($r = -0.71$, $P = 0.008$) and *Xanthidium armatum* ($r = -0.85$, $P = 0.0001$). Neither precipitation nor the drought factor alone (coded as a binary variable) was significant. By contrast, in the mesotrophic Pool 2 neither of the climatic factors was significantly correlated with species composition, whereas the desiccation factor was closely related to the species composition in this pool (Table 1). There was no significant correlation among climatic factors and species diversity indices on either locality.

Morphometric data

There were consistently bigger cells in Pool 1 samples than in Pool 2 (Fig. 3b). We can see an increase of the average cell volume of desmids at both localities in relation to the drought period. In addition, there was a decrease in the average cell volume of desmids in Pool 1 at the end of both summer seasons. By contrast, there was a maximum in the harsh winter of January 2010 and a lower peak in January 2009. Desmid cell volumes in the mesotrophic Pool 2 peaked at the climax of the drought period in spring 2009 and for the second time and less conspicuously in mid-winter 2010. The community biovolume means in Pool 1 were significantly related to the temperature data indicators (Table 1). This correlation was stronger when the weather data were expressed as number of frost days or as the number of days with snow cover. Consequently, the desmid cell volumes from the acidic Pool 1 were not significantly related solely with the drought period coded as the binary variable. On the other hand, the biovolume data of the mesotrophic Pool 2 were not related to the climatic factors, but they were significantly related to the drought period.

The species' S:V ratios ranged from 0.07 μm^{-1} in *Actinotaenium turgidum* to 1.08 μm^{-1} in *Teilingia granulata* (Fig. 4; Supplementary Table 5). The average S:V ratios of the desmid community in Pool 1 were consistently lower than in the second locality (Fig. 3c). Values were relatively stable in the acidic Pool 1 during the entire period of investigation. By contrast, the S:V ratios of the desmids in the more neutral Pool 2 heavily fluctuated in relation to the drought period. They decreased sharply in spring 2009 following the prolonged desiccation of the locality, but were replaced by a rapid increase of these values at the end of the drought period, when the pool was being gradually re-wetted. In addition, morphological disparity, a measure of the shape diversity of samples, decreased considerably in the desmid assemblages of Pool 2 in relation to the drought period (Fig. 3d; Table 1). This trend was not corroborated by the acidic community of Pool 1, where disparity increased in the winter season 2008/2009 as well as in the mid-winter sample of January 2010, and the correlation with the desiccation factor was not significant. However, the disparity values of the mesotrophic Pool 2 were generally higher, with the exception of spring 2009 at the end of the drought period. The morphological turnover, a measure of the change of the average shape characteristics of desmid assemblages between successive samples, reached its maximum in Pool 2 at the end of the dry period (Fig. 3e).

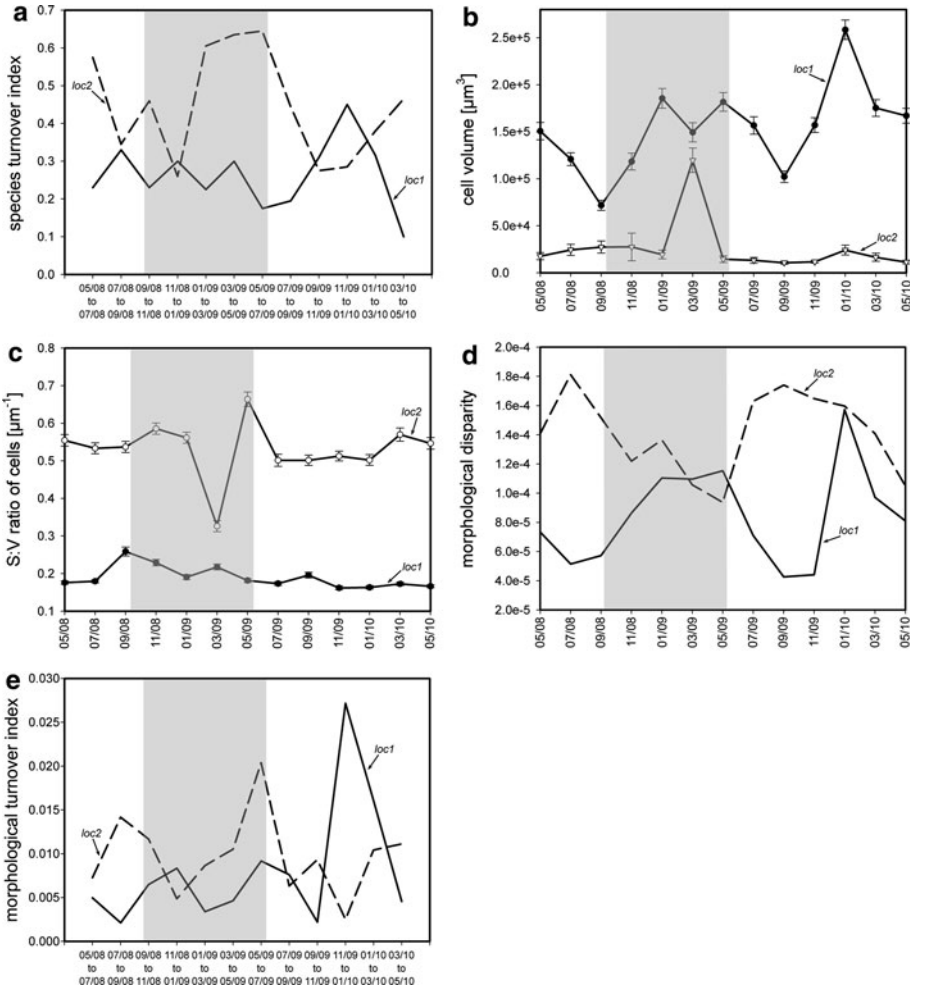

Fig. 3 The temporal dynamics of different species compositions and morphometric data based on the characteristics of samples. *Error bars* represent the standard errors of the mean values of 200 analysed cells. **a** Turnover in species composition between successive samples, **b** mean cell volumes, **c** mean S:V ratio, **d** morphological disparity, **e** morphological turnover between successive samples. The *grey section* emphasizes the drought period

By contrast, the acidic Pool 1 reached the highest morphological turnover value in relation to the harsh winter conditions of the 2009/2010 season. In Pool 1 there was a strongly significant correlation of temperature data with the morphological distance of desmid assemblages from individual samples (expressed as the matrix of Euclidean distances among sample means in the morphospace) (Table 1). This correlation was even stronger when the climatic data were expressed as the number of frost days or the number of days with snow cover. Neither precipitation nor the drought factor alone (coded as a binary variable) was significant. On the other hand, in Pool 2 neither of the climatic factors was significantly correlated with the morphological characteristics, whereas the desiccation factor significantly influenced the morphological similarities of the desmid assemblages in this pool (Table 1). Similarly, morphological disparity (=morphological diversity)

Table 1 The Mantel tests and linear correlation analyses of community species structure/disparity indicators and climatic factors

	Analysis	Mean temperature	Mean daily maximum temperature	Mean daily minimum temperature	Frost days	Snow cover days	Precipitation	Desiccation
Pool 1								
Species composition	Mantel test	**0.29***	**0.29***	**0.31***	**0.38***	**0.42***	$-0.16^{n.s.}$	$0.07^{n.s.}$
Morphological distance of samples	Mantel test	**0.45****	**0.43***	**0.49****	**0.66****	**0.77****	$-0.03^{n.s.}$	$0.06^{n.s.}$
Morphological disparity	Linear correlation	**−0.69****	**−0.67****	**−0.73****	**0.76****	**0.82****	$-0.15^{n.s.}$	$0.44^{n.s.}$
Mean community biovolumes	Linear correlation	**−0.63***	**−0.61***	**−0.66***	**0.71****	**0.74****	$-0.06^{n.s.}$	$0.08^{n.s.}$
Pool 2								
Species composition	Mantel test	$-0.21^{n.s.}$	$-0.19^{n.s.}$	$-0.23^{n.s.}$	$-0.24^{n.s.}$	$-0.21^{n.s.}$	$-0.08^{n.s.}$	**0.42****
Morphological distance of samples	Mantel test	$0.08^{n.s.}$	$0.07^{n.s.}$	$0.11^{n.s.}$	$-0.04^{n.s.}$	$0.04^{n.s.}$	$0.24^{n.s.}$	**0.26***
Morphological disparity	Linear correlation	$0.22^{n.s.}$	$0.21^{n.s.}$	$0.25^{n.s.}$	$0.00^{n.s.}$	$0.02^{n.s.}$	$-0.08^{n.s.}$	**−0.67***
Mean community biovolumes	Linear correlation	$-0.26^{n.s.}$	$-0.27^{n.s.}$	$-0.22^{n.s.}$	$0.13^{n.s.}$	$0.23^{n.s.}$	$-0.09^{n.s.}$	**0.45***

The Mantel tests are represented by the *R*-statistics values, and the linear correlations by Pearson's *r* values. Significant values are depicted in bold

Significances are given by the *P*-values: ** *P*-value <0.01, * *P*-value 0.01–0.05, $^{n.s.}$ *P*-value >0.05

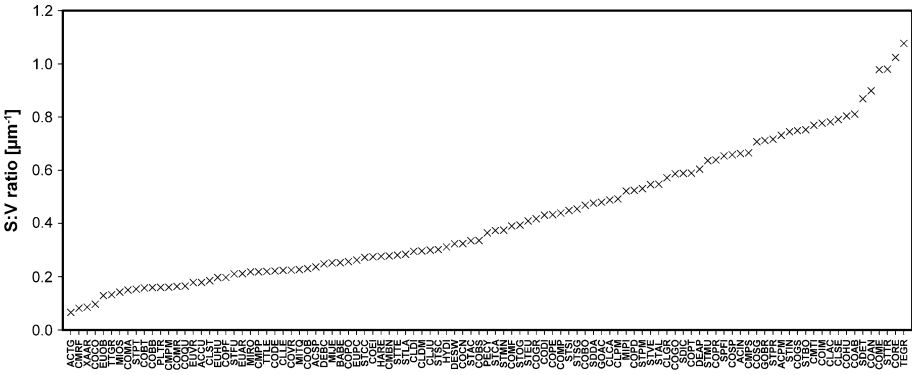

Fig. 4 The S:V ratios of individual species. For species abbreviations see Supplementary Tables 2 and 3

significantly correlated with climatic data in the acidic Pool 1, but such correlations were not significant in Pool 2.

Discussion

After 75 years since Mattauch's (1936) study was published, this peat bog still remains an extremely valuable refuge of desmidiacean diversity. Several very rare species (e.g. *Micrasterias pinnatifida*, *Cosmarium ralfsii* and *C. pseudoretusum*) or species with restricted temperate Eurasian distribution (Coesel 1996; Coesel and Krienitz 2008), such as *M. oscitans* and *Euastrum verrucosum*, occurred at the localities. In addition, there were 20 species detected with the highest sensitivity or rarity values of the NCV index (Coesel and Meesters 2007). Therefore, the desiccation-related disturbance of these assemblages is of interest in the context of the biodiversity conservation of Desmidiales as a whole. Despite being part of a single bog, the desmid communities of the two sites monitored for 25 months differed in many ways. The acidic Pool 1 had generally larger cells, lower S:V ratios, lower diversity and disparity values and mostly lower turnover indices than the more pH-neutral Pool 2. In addition, desmid assemblages in Pool 1 were remarkably stable because they were not temporally autocorrelated at all. However, the drying event influenced the species composition of both pools because the samples taken during the drought period formed relatively consistent groups in the ordination spaces (Fig. 1). This pattern was much more pronounced in the more diversified Pool 2 because there were abrupt changes in the desmid community indicators of this pool (e.g. S:V ratio, turnover indices) by the end of the drought period in spring 2009. Remarkably, the species composition of both localities returned relatively rapidly to their pre-drought situation following the re-wetting of the bog. In the acidic Pool 1, the drying event even led to an increase in the frequency of some rare species with high rarity and sensitivity values of the NCV index in this pH category (Coesel and Meesters 2007). This phenomenon was possibly primarily related to an observed increase in pH values of this pool in relation to the drying event, and subsequent decrease in dominance of *Tetmemorus laevis* at the locality. In this period, most of the water supply resulted from precipitation and was, therefore, less H+ saturated than the groundwater sources. By contrast, the mesotrophic Pool 2 experienced a decrease in diversity values in relation to the

desiccation of the habitat. Apart from that, this locality generally had higher turnover values, both in terms of species turnover and morphological turnover. In this respect, we can presume that the generally more dynamic conditions on this locality were also reflected by its stronger reaction to water level changes. The desmid community composition of the acidic Pool 1 reflected the seasonal meteorological conditions, and its diversity and disparity indicators were more influenced by freezing winter conditions than by the water levels. We can summarise that the desmid communities of the investigated locality proved to be able to cope with the aperiodic drying event of their habitats. The evolutionary point of view suggests that the benthic desmid species have generally been well adapted to such extreme drought events. There was, however, a more pronounced shift in species composition in the second half of the drought period (especially in Pool 2), reflected especially by an increase in average cell volumes. Therefore, we can assume that, had the drying event continued for a longer time period, the desmid communities might have been considerably changed. We cannot also preclude that they might be more severely influenced in the case of more frequent and repeated drying events. Desmids have been found to be strongly negatively influenced by the long-term terrestrialisation of peatlands (Mataloni 1999; Borics et al. 2003; Wayda 2004), and the desmid flora of the investigated peat bog would certainly be impoverished by continuous low groundwater levels. From a conservation point of view, we can state that the aperiodic drying event of the minerotrophic peat bog lasting for about 8 months in 2008 and 2009 did not negatively influence its rich and unique desmid assemblages. However, we have to emphasise that more frequent or longer drought periods might have a much more severe impact on the desmidiacean phytobenthos of the locality. Interestingly, we did not observe desmid zygospores in the course of the study. Evans (1959) reported several desmid species that were able to survive the prolonged dry periods in their vegetative cell stage. Those cells, however, did not reproduce prior to the re-wetting of their habitat. We cannot preclude that zygospores were also formed by some desmids at our localities, but, in such a case, their frequencies must have remained very low in comparison with the vegetative cells of other species and therefore were not detected. Similarly, the drought-related lower diversity values, observed in the species-rich mesotrophic Pool 2, might be explained by a decrease in the absolute abundances of some species (e.g. *Closterium calosporum* var. *brasiliense* or *Micrasterias pinnatifida*). These might have survived the dry period in very low cell numbers, but increased steadily after the re-wetting of the pool. In other words, these species seemingly "disappeared" as a result of a drying event, but they apparently did not really become extinct at the locality. Even if our study was not primarily designed for the detection of periodic patterns in species distribution, we found significant seasonal changes in Pool 1, whose species compositions as a whole were related to the temperature data. Interestingly, the number of frost days and the number of snow cover days were better predictors of biotic data than the actual mean, minimum or maximum temperatures. These results indicate that the periodicity of benthic peat bog desmids might primarily rely on winter disturbances caused by the prolonged periods of darkness and/or anoxic conditions developing on the bottom of frozen pools in temperate or boreal ecosystems. Machová-Černá and Neustupa (2009) reported that the winter disturbance significantly altered community structure of peat bog benthic microalgae. The data presented in this study, illustrating the profound effects of a prolonged freezing of sites in the 2009/2010 winter season, corroborate our previous results. However, the more precise effects of seasonal winter disturbance on peat bog microphytobenthos need to be investigated in studies specifically targeting this issue. Possible differences in these patterns among peat

bog wetlands with differing temperature amplitudes, and, consequently, with widely different proportions of winter frost days might be of special interest.

Apart from traditional species data, we also used morphological disparity indicators and S:V values based on the morphometric data of individual species. The disparity indicators were employed in the similar way as in our recent study on desmidiacean disparity patterns in Central European peatlands (Neustupa et al. 2009). These disparity-based measures illustrated more or less similar, but generally much more pronounced, temporal or desiccation-related trends than the traditional species data. We can see that in the drought period and in the harsh winter of 2009/2010 the disparity data of the acidic Pool 1 increased more sharply than the species richness values (Figs. 2a, 3d). Similarly, the morphospace turnover increased more abruptly between successive samples in the more pH-neutral Pool 2 by the end of the drought period than the comparative species-based turnover index (Fig. 3a, e). These trends indicate that the change in morphological features of the investigated assemblages often exceeded their species composition changes. In other words, species increasing or decreasing in frequency in response to these environmental events were mutually more morphologically different than the average shape dissimilarity was among the species of the assemblages. In this way, the morphometric approach allowed us to detect these differences, which would have otherwise remained invisible from the species data alone. Apart from the disparity analysis, we used the morphometric data for the estimation of the surface and volume values of individual species. Previously, desmids were rarely included in the biovolume or S:V analyses of microalgae (but see e.g. Martínez-Almeida and Tavera 2005). The widely used geometric formulas of Hillebrand et al. (1999) and Sun and Liu (2003) have mostly been intended for the surface and volume estimation of planktonic microalgae. Hillebrand et al. (1999) suggested the ellipsoid- and cone-based geometric formulas for desmid genera, but also pointed out that their applications might be problematic in species with lobulated outlines. The ellipsoid-based formulas generally greatly overestimated the volume values of biradiate species (such as e.g. *Cosmarium pseudoretusum*, *Euastrum oblongum* or *Micrasterias pinnatifida*) and underestimated their surface values. This drawback can now be overcome by the application of morphometric landmark-based data that could result in more reliable surface and volume values. We believe that our method of surface and volume estimation could be useful in future studies of microalgal phytobenthos, not only for desmids but possibly also for diatoms, where the geometric formulas also might result in unreliable results in taxa with complex outlines (e.g. some *Cymbella* or *Eunotia* species). The actual S:V values estimated for individual desmid species in this study ranged from 0.07 μm^{-1} in *Actinotaenium turgidum* to 1.08 μm^{-1} in *Teilingia granulata*, giving values generally compatible with published data for benthic diatoms (Snoeijs et al. 2002) or freshwater phytoplankton (Caputo et al. 2008). Interestingly, species with the largest cells (such as *Micrasterias rotata* or *Closterium* spp.) had intermediate S:V values thanks to their shape properties. Maintaining the S:V values within the limits typical for other microalgae has probably been one of the important factors in the complicated morphological evolution of Desmidiales, especially in species with relatively large cells.

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Supplementary material. Surface and volume estimation of biradiate desmid cells.

1. The 2D landmark configurations spanning the frontal views of the cells were used for the computation of their actual area (A_x) and perimeter (P_x) values in TpsDig, ver. 2.15. In addition, the length (a) and width (b) of the cells was also measured in TpsDig, ver. 2.15.
2. The maximum thickness of the cells (c) was estimated according to the width-to-thickness ratios of individual species.
3. The volume of a general ellipsoid ($V_{ellipsoid}$) with given a, b, and c values and the area of an ellipse with a and b axes were computed.
4. Then, the volume of a cell (V_x) with a generally ellipsoidal layout was approximated on the basis of the formula $V_x/V_{ellipsoid} = A_x/A_{ellipse}$, i.e. $V_x = (A_x \,.\, V_{ellipsoid})/A_{ellipse}$. Hence, after the algebraic simplification of trivial geometric formulas for scalene ellipsoids it gave $V_x = (2 \,.\, A_x \,.\, c)/3$.
5. Similarly, the surfaces of cells with general ellipsoidal layouts were approximated on the basis of the following formula $S_x = (P_x \,.\, S_{ellipsoid})/P_{ellipse}$. The perimeter of an ellipse with a and b axes was estimated using Muir´s approximation (Sykora 2005) as $P_{ellipse} \approx 2 \,.\, \pi \,.\, [(a^{3/2} + b^{3/2})/2]^{2/3}$, giving the maximum error rate of 1.046%. The surface of a general (scalene) ellipsoid was approximated using Knud Thomsen´s formula as $S_{ellipsoid} \approx 4 \,.\, \pi \,.\, [(a^p.b^p + a^p.c^p + b^p.c^p)/3]^{1/p}$, where $p = 1.6075$, giving the maximum error rate of 1.061% (Michon 2009).
6. In species with generally cylindrical layouts (e.g. species of *Pleurotaenium, Haplotaenium or Hyalotheca*) the surface and volume values were estimated in a similar way, but the 2D landmark configurations were compared with the areas and perimeters of rectangles with a and b sides. Accordingly, the comparative surface and volume values were acquired from the cylinders of b diameters and b heights. The accuracy of this S:V estimation was evaluated by an analysis of a wide test set of geometric solids including ellipsoids, cylinders, cuboids and bipyramids with varying shapes and sizes (data not shown).

Supplementary table 1. Abiotic data of individual samples.

Sample date	T (°C)	T_{max} (°C)	T_{min} (°C)	Frost days	Snow cover days	Precipitation (mm)	Water depth Pool 1	Water depth Pool 2	pH Pool 1	pH Pool2	Conductivity Pool 1 ($\mu S.cm^{-1}$)	Conductivity Pool 2 ($\mu S.cm^{-1}$)
12-5-08	10.36	15.71	4.36	2	0	51.8	15	7	5.3	6.7	110	220
9-7-08	17.73	23.48	11.48	0	0	37.3	12	7	5.2	6.6	72	246
21-9-08	14.83	20.03	9.54	0	0	30.5	10	3	6.1	6.8	355	381
25-11-08	5.25	8.31	1.43	6	5	48.3	0	0	-	-	-	-
15-1-09	-3.37	-1.24	-6.25	23	12	17.3	0	0	-	-	-	-
26-3-09	3.75	6.84	0.72	8	10	37.4	0	0	-	-	-	-
21-5-09	13.57	19.05	7.46	0	0	44.7	0	0	5.8	6.8	426	270
24-7-09	18.68	24.46	14.10	0	0	113.0	10	10	5.3	7.0	94	208
29-9-09	15.1	20.48	10.22	0	0	12.9	12	9	5.2	7.0	89	228
23-11-09	6.02	9.16	3.14	3	1	31.7	18	7	5.1	6.5	102	269
29-1-10	-4.22	-2.11	-7.53	29	30	14.7	14	10	4.9	6.4	75	231
31-3-10	8.21	13.58	2.62	4	10	46.2	20	12	5.3	6.8	88	265
19-5-10	10.90	15.59	5.82	2	0	48.5	17	9	4.8	7.2	79	289

Supplementary table 2. Species data of samples taken from the Pool 1.

POOL 1		K-W significance[1]	12-05 2008	09-07 2008	21-09 2008	25-11 2008	15-01 2009	26-03 2009	21-05 2009	24-07 2009	29-09 2009	23-11 2009	29-01 2010	31-03 2010	19-05 2010
Actinotaenium cucurbita	ACCU		0	0	0	1	1	2	0	0	2	1	1	1	3
Bambusina brebissonii	BABE		12	0	0	2	0	0	0	0	0	0	0	0	0
Closterium calosporum	CLCA		0	0	0	0	1	1	0	1	0	0	0	1	0
Closterium dianae var. minus	CLDM		0	0	0	1	0	0	1	0	0	0	0	0	0
Closterium gracile	CLGR		0	0	7	4	0	0	0	0	0	0	0	0	0
Closterium juncidum	CLJU	**	0	0	16	9	8	18	2	0	0	1	0	0	0
Closterium lineatum var. elongatum	CLLE	*	0	0	1	4	3	1	0	0	0	0	0	0	0
Closterium setaceum	CLSE		0	0	0	1	0	0	0	0	0	0	0	0	0
Closterium striolatum	CLST		33	18	3	11	7	16	2	1	1	4	4	4	11
Cosmarium blytii var. novae-silvae	CMBN		0	1	0	0	1	4	0	0	0	0	0	0	0
Cosmarium prominulum var. subundulatum	CMPS		1	0	0	1	2	0	0	0	2	2	0	0	0
Cosmarium pseudopyramidatum	CMPP		0	0	0	0	1	0	0	0	0	0	0	0	0
Cosmarium pyramidatum	CMPM		0	0	1	0	0	0	0	0	1	0	0	0	0
Cosmarium ralfsii	CMRF		4	1	0	2	4	3	7	5	0	2	9	6	3
Cosmarium tinctum	CMTI		0	0	0	0	0	2	0	1	3	0	0	0	0
Euastrum humerosum	EUHU		0	0	0	0	0	1	0	0	0	0	0	0	0
Haplotaenium rectum	HARE		1	0	0	0	1	0	0	0	0	0	0	0	0
Hyalotheca dissiliens	HYDI		0	0	0	1	0	0	0	0	0	0	0	0	0
Micrasterias jennerii	MIJE		13	8	6	16	33	27	29	15	4	8	49	32	24
Micrasterias oscitans	MIOS		0	0	1	5	3	5	7	8	1	2	11	3	0
Micrasterias truncata var. quadrata	MITQ		6	4	1	3	5	2	10	6	3	1	12	4	4
Penium cylindrus	PECY	*	0	3	10	10	2	1	3	0	1	0	1	0	0
Staurastrum scabrum	STSC		0	0	1	1	0	0	0	0	0	0	0	0	0
Staurastrum simonyi	STSI	**	0	2	3	5	1	8	6	0	3	0	0	2	2
Staurastrum teliferum	STTE		0	0	0	0	0	0	0	0	0	1	0	0	0
Staurodesmus incus	SDIC		0	0	8	5	2	4	0	0	0	1	0	0	0
Teilingia granulata	TEGR		0	0	4	0	0	0	0	0	0	0	0	0	0
Tetmemorus granulatus	TTGR	**	79	91	51	50	71	49	90	95	87	129	76	106	114
Tetmemorus laevis	TTLE		39	67	86	59	32	40	33	60	88	37	5	35	30
Xanthidium armatum	XAAR		12	5	1	9	22	16	10	8	4	11	32	6	9

[1] The K-W significances indicate the *p*-values of the Kruskal-Wallis tests for the differences in medians of species relative abundances in the drought and wet periods. *** *p*-value < 0.01, ** *p*-value 0.01 to 0.05, * *p*-value 0.05 to 0.1

Supplementary table 3. Species data of samples taken from the Pool 2.

POOL 2		K-W significance[1]	12-05 2008	09-07 2008	21-09 2008	25-11 2008	15-01 2009	26-03 2009	21-05 2009	24-07 2009	29-09 2009	23-11 2009	29-01 2010	31-03 2010	19-05 2010
Actinotaenium inconspicuum	ACIN		0	0	0	0	0	0	0	2	1	0	0	1	1
Actinotaenium perminutum	ACPM		2	2	1	0	0	0	4	1	2	0	1	3	2
Actinotaenium turgidum	ACTG		1	4	5	0	1	19	1	1	0	0	3	2	0
Actinotaenium sp.	ACSP		0	0	0	0	0	0	1	0	0	0	0	0	0
Closterium acutum	CLAC		1	0	0	0	0	0	0	1	0	0	0	1	0
Closterium calosporum var. brasiliense	CLPM	**	32	15	39	14	12	4	0	15	42	50	50	24	3
Closterium dianae	CLDI		1	13	12	3	16	3	2	16	5	14	15	8	0
Cosmarium abbreviatum	COAB		1	0	0	0	0	0	0	0	0	0	5	0	0
Cosmarium angulosum	COAN		0	1	1	2	2	0	1	3	2	3	2	2	5
Cosmarium cf. basiornatum	COBS		0	0	0	1	0	0	0	1	0	1	0	7	1
Cosmarium bioculatum var. depressum	COBO		4	0	0	0	0	0	0	0	1	2	0	1	0
Cosmarium botrytis var. botrytis	COBB		4	0	2	4	3	2	1	0	1	0	0	0	3
Cosmarium botrytis var. tumidum	COBT	*	5	1	4	5	4	31	4	1	0	1	5	1	1
Cosmarium connatum	COCO		1	3	1	0	2	1	1	0	1	1	2	1	1
Cosmarium contractum	COCN	*	1	4	3	1	2	2	4	2	8	11	7	8	11
Cosmarium depressum	CODE		4	3	2	0	0	0	0	0	0	0	0	0	0
Cosmarium difficile	CODI		0	11	16	4	7	1	13	3	0	1	1	1	2
Cosmarium eichlerianum	COEI		0	0	0	0	0	0	0	0	0	0	0	0	1
Cosmarium gonioides	COGO		0	3	1	3	0	0	0	0	0	0	1	1	1
Cosmarium gonioides var. subturgidum	COGS		0	0	0	1	1	0	0	0	1	1	0	0	0
Cosmarium granatum	COGR	**	0	2	0	7	9	7	0	0	0	0	0	0	0
Cosmarium humile	COHU	**	1	8	2	2	0	0	1	10	13	17	9	11	23
Cosmarium impressulum	COIM		0	1	0	0	0	0	0	0	0	0	0	0	0
Cosmarium margaritatum	COMA		0	0	0	1	0	1	0	0	0	0	0	2	3
Cosmarium margaritiferum	COMR		0	1	1	0	0	1	0	0	0	0	0	0	1
Cosmarium medioretusum	COME		0	0	0	0	0	0	0	1	0	1	0	0	1
Cosmarium moniliforme var. panduriforme	COMP		0	0	0	0	0	0	0	0	0	0	0	2	8
Cosmarium monochondrum var. fallax	COMF		14	2	1	0	0	0	0	0	0	0	0	0	0
Cosmarium obtusatum	COOB		0	0	0	0	0	0	3	0	3	0	0	0	1
Cosmarium paragranatoides	COPR	***	0	1	1	12	16	8	9	0	0	2	7	6	2
Cosmarium perforatum	COPF		0	0	0	0	1	0	0	0	0	0	1	0	1
Cosmarium phaseolus var. elevatum	COPE		6	3	8	1	0	12	1	4	4	5	2	5	12
Cosmarium polygonum var. depressum	COPD		13	0	0	2	0	0	0	3	1	0	0	0	23
Cosmarium pseudoornatum	COPO		0	0	0	0	0	0	0	0	1	0	0	0	0
Cosmarium pseudoretusum	COPT	**	1	28	19	45	44	20	36	28	16	17	33	31	25
Cosmarium quadratum	COQU		0	0	0	0	0	0	0	1	1	1	0	0	0
Cosmarium regnellii	CORE		16	4	9	17	12	0	53	9	2	0	5	15	7
Cosmarium sp.	COSP		26	0	1	8	7	0	0	0	2	1	0	0	8
Cosmarium subgranatum	COSG	*	1	7	19	21	7	5	26	8	3	2	1	6	4
Cosmarium varsoviense	COVR		0	0	0	0	0	1	1	0	0	1	0	2	1

Desmidium aptogonum	DEAP		9	9	0	2	7	1	0	3	1	4	2	2	0
Desmidium baileyi var caelatum	DEBC		0	0	0	0	0	0	0	5	0	0	0	0	0
Desmidium swartzii	DESW	*	0	10	0	0	0	0	0	1	12	1	0	7	1
Euastrum ansatum var. rhomboidale	EUAR		0	1	1	2	0	7	2	2	0	2	1	5	4
Euastrum oblongum	EUOB		0	0	0	0	1	6	0	0	0	0	0	0	0
Euastrum pectinatum	EUPC	**	0	0	1	1	3	19	6	1	2	1	4	0	1
Euastrum verrucosum	EUVR		0	0	0	0	0	1	0	0	0	0	0	0	0
Gonatozygon aculeatum	GOAC		0	0	0	0	0	0	0	1	4	4	0	1	0
Gonatozygon brebissonii	GOBR		3	0	0	0	0	0	0	0	0	0	0	0	0
Haplotaenium rectum	HARE		0	0	0	0	0	0	1	0	1	0	1	0	0
Hyalotheca dissiliens	HYDI		3	0	0	7	0	0	0	48	25	6	4	1	10
Micrasterias pinnatifida	MIPI		1	1	0	3	0	0	0	0	0	2	0	0	1
Micrasterias rotata	MIRO		0	0	0	1	0	0	0	0	0	0	0	0	0
Pleurotaenium cf. trabecula	PLTR	*	2	2	1	2	1	17	2	1	1	0	1	1	0
Sphaerozosma filiforme	SPFI		9	10	15	1	9	0	0	0	16	10	0	0	0
Staurastrum aculeatum	STAC		0	0	0	0	0	0	0	0	0	1	0	0	0
Staurastrum alternans	STAL	**	1	2	1	1	2	1	0	6	4	6	5	9	4
Staurastrum boreale	STBO		0	1	0	0	0	2	0	0	0	0	0	0	0
Staurastrum crassangulatum	STCA	*	0	6	1	0	0	0	1	3	1	1	0	5	1
Staurastrum cristatum var. cuneatum	STCC		0	0	0	0	0	1	0	0	0	0	0	0	0
Staurastrum eurycerum	STEU		0	1	0	0	0	0	0	0	0	1	0	0	0
Staurastrum furcigerum	STFU		4	0	2	0	0	2	2	1	0	0	2	0	0
Staurastrum inflexum	STIN		1	0	0	0	0	0	0	2	2	1	1	0	0
Staurastrum lapponicum	STLA	*	3	2	1	4	4	8	3	1	2	4	6	1	1
Staurastrum manfeldtii	STMN		1	0	0	1	1	3	2	3	11	12	11	7	8
Staurastrum muticum	STMU		0	0	0	0	0	0	0	3	0	1	0	0	2
Staurastrum oligacanthum	STOG		0	0	0	0	0	0	0	1	0	1	0	0	0
Staurastrum polymorphum	STPM		0	0	0	1	0	1	0	0	0	0	0	2	0
Staurastrum polytrichum	STPT		0	1	0	0	0	0	0	0	0	0	0	0	0
Staurastrum pseudotetracerum	STPR		19	31	21	18	23	8	18	4	3	3	7	2	2
Staurastrum sebaldi var. gracile	STSG		0	0	1	0	0	3	0	0	0	0	0	1	7
Staurastrum teliferum	STTE		2	1	0	0	1	0	0	0	0	0	1	0	1
Staurastrum tetracerum	STTR	**	1	2	2	0	1	0	0	0	1	2	2	6	3
Staurastrum vestitum	STVE		0	0	0	0	1	2	1	0	0	2	2	0	0
Staurodesmus dejectus var. apiculatus	SDDA		6	3	5	2	0	0	0	1	1	0	0	0	0
Staurodesmus extensus	SDET		0	0	0	0	0	0	0	0	0	0	0	4	1
Teilingia granulata	TEGR		0	0	0	0	0	0	0	3	3	2	0	5	1
Tetmemorus granulatus	TTGR		0	0	0	0	0	0	0	0	0	1	0	0	0

[1] The K-W significances indicate the *p*-values of the Kruskal-Wallis tests for the differences in medians of species relative abundances in the drought and wet periods. *** *p*-value < 0.01, ** *p*-value 0.01 to 0.05, * *p*-value 0.05 to 0.1

Supplementary table 4. SIMPER analyses, species responsible for the differentiation of desmid communities in dry and wet periods.

Pool 1 (acidic site)				
Taxon	Contribution to the overall discrimination	Cumulative discrimination (%)	Mean abundance (dry period)	Mean abundance (wet period)
Tetmemorus granulatus	7.96	24.4	65.0	92.0
Tetmemorus laevis	5.82	42.2	41.0	49.7
Micrasterias jenneri	3.85	53.9	26.3	17.7
Closterium juncidum	2.24	60.8	9.3	1.9
Xanthidium armatum	2.22	67.6	14.3	9.8
Closterium striolatum	2.17	74.2	9.0	8.8
Micrasterias oscitans	1.03	77.4	5.0	2.9
Staurastrum simonyi	1.01	80.5	5.0	1.3
Penium cylindrus	0.96	83.4	4.0	1.7
Micrasterias truncata var. *quadrata*	0.86	86.0	5.0	4.6
Pool 2 (neutral site)				
Taxon	Contribution to the overall discrimination	Cumulative discrimination (%)	Mean abundance (dry period)	Mean abundance (wet period)
Closterium calosporum var. *brasiliense*	5.92	9.8	7.5	30.0
Cosmarium regnellii	4.29	16.9	20.5	7.4
Cosmarium pseudoretusum	4.19	23.8	36.3	22.0
Staurastrum pseudotetracerum	2.87	28.6	16.8	10.2
Cosmarium subgranatum	2.73	33.1	14.8	5.7
Hyalotheca dissiliens	2.65	37.5	1.8	10.8
Cosmarium humerosum	2.44	41.5	0.8	10.4
Cosmarium paragranatoides	2.29	45.3	11.3	2.11
Cosmarium botrytis var. tumidum	2.28	49.1	11.0	2.11
Closterium dianae	1.85	52.1	6.0	9.3

Supplementary table 5. The surface and volume values estimated for individual species on the basis of morphometric analysis.

Taxon	Abbreviation	Surface (μm^2)	Volume (μm^3)	S:V (μm^{-1})
Actinotaenium turgidum	ACTG	37428.9	567104.2	0.066
Cosmarium ralfsii	CMRF	55360.7	675130.3	0.082
Xanthidium armatum	XAAR	40230.6	467798.2	0.086
Cosmarium connatum	COCO	15165.4	156343.9	0.097
Euastrum oblongum	EUOB	77983.6	604524.0	0.129
Tetmemorus granulatus	TTGR	21135.8	158915.6	0.133
Micrasterias oscitans	MIOS	40251.4	283460.7	0.142
Cosmarium margaritatum	COMA	14782.7	98551.6	0.150
Staurastrum polytrichum	STPT	18900.7	122731.7	0.154
Cosmarium botrytis var. tumidum	COBT	17120.7	108358.6	0.158
Cosmarium botrytis var. botrytis	COBB	23569.2	148233.7	0.159
Pleurotaenium cf. trabecula	PLTR	32765.3	204783.0	0.160
Cosmarium pyramidatum	CMPM	14003.3	86977.0	0.161
Cosmarium margaritiferum	COMR	15267.9	93097.1	0.164
Cosmarium quadratum	COQU	7968.2	48292.2	0.165
Euastrum verrucosum	EUVR	26542.0	148279.6	0.179
Actinotaenium cucurbita	ACCU	4270.6	23858.2	0.179
Closterium striolatum	CLST	19354.8	104620.8	0.185
Euastrum humerosum	EUHU	16717.6	84861.0	0.197
Cosmarium perforatum	COPF	8995.3	45430.6	0.198
Staurastrum furcigerum	STFU	19374.2	91820.9	0.211
Euastrum ansatum var. rhomboidale	EUAR	12649.9	59951.9	0.211
Micrasterias rotata	MIRO	633238.1	2904762.0	0.218
Cosmarium pseudopyramidatum	CMPP	3853.2	17675.2	0.218
Tetmemorus laevis	TTLE	6504.6	29566.4	0.220
Cosmarium depressum	CODE	9427.6	42466.8	0.222
Closterium lineatum var. elongatum	CLLE	35626.9	159048.5	0.224
Cosmarium varsoviense	COVR	4428.6	19682.6	0.225
Micrasterias truncata var. quadrata	MITQ	41813.0	184198.4	0.227
Cosmarium obtusatum	COOB	8199.9	35497.5	0.231
Actinotaenium sp.	ACSP	2442.6	10306.4	0.237
Desmidium baileyi var caelatum	DEBC	5601.7	22587.7	0.248
Micrasterias jenneri	MIJE	65041.9	258102.8	0.252
Bambusina brebissonii	BABE	3050.2	12056.0	0.253
Cosmarium pseudoornatum	COPO	5463.5	21258.7	0.257
Euastrum pectinatum	EUPC	8793.1	33433.8	0.263

Staurastrum cristatum var. cuneatum	STCC	5193.2	19022.8	0.273
Cosmarium eichlerianum	COEI	3995.4	14528.7	0.275
Haplotaenium rectum	HARE	14395.7	51970.0	0.277
Cosmarium blytii var. novae-silvae	CMBN	3420.7	12304.6	0.278
Staurastrum teliferum	STTE	5174.7	18349.9	0.282
Staurastrum lapponicum	STLA	5283.2	18537.7	0.285
Closterium dianae	CLDI	11306.8	38328.1	0.295
Closterium dianae var. minus	CLDM	11335.5	38166.6	0.297
Closterium juncidum	CLJU	9594.2	31980.5	0.300
Staurastrum scabrum	STSC	5310.1	17525.0	0.303
Hyalotheca dissiliens	HYDI	1874.2	6007.0	0.312
Desmidium swartzii	DESW	3780.9	11669.3	0.324
Cosmarium contractum	COCN	2588.3	7963.8	0.325
Staurastrum aculeatum	STAC	4964.3	14818.9	0.335
Cosmarium cf. basiornatum	COBS	3082.9	9175.2	0.336
Penium cylindrus	PECY	1664.4	4560.0	0.365
Staurastrum crassangulatum	STCA	3160.9	8451.7	0.374
Staurastrum manfeldtii	STMN	9097.9	24261.1	0.375
Cosmarium monochondrum var. fallax	COMF	1673.7	4280.5	0.391
Staurastrum oligacanthum	STOG	2481.2	6297.4	0.394
Staurastrum eurycerum	STEU	4095.4	9988.9	0.410
Cosmarium granatum	COGR	2375.8	5683.7	0.418
Cosmarium difficile	CODI	1508.2	3491.1	0.432
Cosmarium phaseolus var. elevatum	COPE	1895.6	4377.9	0.433
Cosmarium moniliforme var. panduriforme	COMP	913.8	2081.6	0.439
Staurastrum simonyi	STSI	2173.6	4841.0	0.449
Staurastrum sebaldi var. gracile	STSG	3812.2	8378.5	0.455
Cosmarium bioculatum var. depressum	COBO	1501.3	3201.1	0.469
Staurodesmus dejectus var. apiculatus	SDDA	2372.1	4983.5	0.476
Gonatozygon aculeatum	GOAC	3422.9	7131.0	0.480
Closterium calosporum	CLCA	3792.9	7772.3	0.488
Closterium calosporum var. brasiliense	CLPM	3651.2	7406.1	0.493
Micrasterias pinnatifida	MIPI	16131.6	30903.5	0.522
Cosmarium polygonum var. depressum	COPD	1136.2	2164.1	0.525
Staurastrum polymorphum	STPM	2146.2	4041.9	0.531
Staurastrum vestitum	STVE	1756.3	3216.6	0.546
Staurastrum alternans	STAL	1506.2	2748.5	0.548
Closterium gracile	CLGR	4238.9	7410.7	0.572
Cosmarium gonioides	COGO	446.2	760.2	0.587
Staurodesmus incus	SDIC	1010.1	1717.9	0.588
Cosmarium pseudoretusum	COPT	1583.8	2688.9	0.589

Desmidium aptogonum	DEAP	1273.8	2108.9	0.604
Staurastrum muticum	STMU	1062.7	1670.9	0.636
Cosmarium paragranatoides	COPR	1051.0	1644.8	0.639
Sphaerozosma filiforme	SPFI	878.7	1343.6	0.654
Cosmarium sp.	COSP	574.3	871.4	0.659
Actinotaenium inconspicuum	ACIN	372.4	561.7	0.663
Cosmarium prominulum var. subundulatum	CMPS	582.6	874.8	0.666
Cosmarium subgranatum	COSG	942.0	1332.4	0.707
Gonatozygon brebissonii	GOBR	1631.3	2291.2	0.712
Staurastrum pseudotetracerum	STPR	1845.9	2574.6	0.717
Actinotaenium perminutum	ACPM	247.9	339.1	0.731
Staurastrum inflexum	STIN	1195.1	1604.2	0.745
Cosmarium gonioides var. subturgidum	COGS	272.8	364.2	0.749
Staurastrum boreale	STBO	1662.9	2208.4	0.753
Cosmarium tinctum	CMTI	471.8	613.5	0.769
Cosmarium impressulum	COIM	681.1	876.6	0.777
Closterium acutum	CLAC	2677.6	3424.1	0.782
Closterium setaceum	CLSE	13649.3	17255.7	0.791
Cosmarium humile	COHU	672.1	836.0	0.804
Cosmarium abbreviatum	COAB	575.4	709.5	0.811
Staurodesmus extensus	SDET	619.5	712.9	0.869
Cosmarium angulosum	COAN	406.2	451.8	0.899
Cosmarium medioretusum	COME	504.4	515.7	0.978
Staurastrum tetracerum	STTR	1514.1	1545.0	0.980
Cosmarium regnellii	CORE	313.9	306.6	1.024
Teilingia granulata	TEGR	335.9	311.9	1.077